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Climatic predictors of species distributions neglect biophysiologically meaningful variables

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Abstract

Aim: Species distribution models (SDMs) have played a pivotal role in predicting how species might respond to climate change. To generate reliable and realistic predictions from these models requires the use of climate variables that adequately capture physiological responses of species to climate and therefore provide a proximal link between climate and their distributions. Here, we examine whether the climate variables used in plant SDMs are different from those known to influence directly plant physiology.

Location: Global.

Methods: We carry out an extensive, systematic review of the climate variables used to model the distributions of plant species and provide comparison to the climate variables identified as important in the plant physiology literature. We calculate the top 10 SDM and physiology variables at 2.5° spatial resolution for the globe and use principal component analyses and multiple regression to assess similarity between the climatic variation described by both variable sets.

Results: We find that the most commonly used SDM variables do not reflect the most important physiological variables and differ in two main ways: (a) SDM variables rely on seasonal or annual rainfall as simple proxies of water available to plants and neglect more direct measures such as soil water content; and (b) SDM variables are typically averaged across seasons or years and overlook the importance of climatic events within the critical growth period of plants. We identify notable differences in their spatial gradients globally and show where distal variables may be less reliable proxies for the variables to which species are known to respond.

Main conclusions: There is a growing need for the development of accessible, fine-resolution global climate surfaces of physiological variables. This would provide a means to improve the reliability of future range predictions from SDMs and support efforts to conserve biodiversity in a changing climate.

KEYWORDS

climate change, conservation, plant physiology, range shifts, species distribution models

1 | INTRODUCTION

Over the last 20 years, species distribution models (SDMs) have become one of the most widely used methods for predicting how species will respond to global environmental change. A search in Web of Science (May 2018) for articles containing both "species distribution models" and "climate change", for example, gave over 7,800 returns. Studies that use SDMs, or develop tools for doing so are amongst the most highly cited in ecology and conservation (e.g., Elith et al., 2006 [3,524 citations]; Guisan & Zimmerman, 2000 [3,479]; Phillips, Anderson, & Schapire, 2006 [4,953]; Thomas et al., 2004 [3,271]—Web of Science Core Collection, May 2018). Moreover, results from SDMs have shaped 21st century conservation policy, highlighting that regions with favourable climates will soon lie beyond the natural limits of colonization of many current species distributions, and hence, that the redesign of protected area networks or species translocations may be needed (Guisan & Thuiller, 2005).

In the context of climate change, a premise of SDMs is that climate determines the natural distribution of species (Pearson & Dawson, 2003). On this basis, SDMs determine the statistical relationship between current species' presence/absence data and a set of climatic variables and use this to predict the areas that a species may be able to occupy in the future (Elith & Leathwick, 2009). The climate variables selected to model species distributions are therefore assumed to impose constraints on species such that at locations or times when climatic conditions are unsuitable, populations of a species are unable to survive in the wild (Pearson & Dawson, 2003).

The climatic variables used in SDMs can be identified in two main ways. Most commonly, a correlative approach is taken, whereby statistical associations between species' presence or absence data and a set of climate variables are initially tested and the strongest predictors included in the SDM (Elith & Leathwick, 2009). In contrast to these "correlative" SDMs, "mechanistic" or "physiological" models use variables for which experimental work has established direct links to biological processes of the study species.

The appropriate selection of climate variables is fundamental to the reliability of SDMs (Austin & Van Neil, 2011). If the variables selected cannot adequately represent climatic factors that influence a species' distribution, then subsequent range predictions in new locations or future climate scenarios may be incorrect. The degree to which climate variables are proximal is therefore an important consideration when constructing SDMs (Austin, 2002; Petitpierre, Broennimann, Kueffer, Daehler, & Guisan, 2017). Proximal variables directly capture physiological mechanisms or processes of the study species and, as such, are causally linked to a species' distributional response to climate both in space and in time (Austin, 2002, 2007).

Indirect links to species' physiology can be captured by "distal" variables which may provide a good "mean field approximation" for these proximal predictors (Bennie, Wilson, Maclean, & Suggitt, 2014). However, other factors in a species' environment, both climatic and non-climatic, may contribute strongly to observed relationships between distal variables and species distributions in correlative models. The influence of these additional factors may be unique to the time and place in which correlations between a distal variable and species distributions are determined so that in new locations or future climates the ability of a distal variable to predict species distributions may weaken or be lost (Jackson, Betancourt, Booth, & Gray, 2009). Proximal variables are thus likely to provide more robust estimates of distribution, particularly when applied to studies of species responses to climate change, and are often considered superior to distal alternatives when using SDMs for this purpose (Austin, 2002).

Despite recommendations to use proximal variables in SDMs (e.g., Helmuth, Kingsolver, & Carrington, 2005; Barbet-Massin & Jetz, 2014), those selected are known often to neglect physiological processes (Mod, Scherrer, Luoto, & Guisan, 2016). By definition, mechanistic SDMs will use proximal variables but correlative SDMs, which remain the most popular approach to modelling species distributions (Barry & Elith, 2006), may use any climate variable deemed to correlate sufficiently to species distributions such that it can predict presence or absence. For plants, it is not yet known how closely the climate variables used most commonly in SDMs compare to those of known physiological importance.

In this study, we quantify the use of climate variables in SDM studies of vascular and non-vascular plants and provide comparison to those identified as physiologically important in the plant physiology literature. We test two hypotheses:

(i) Climate variables used in plant SDMs are different from those known directly to influence plant physiology
(ii) The spatial patterns of climate variation described by the most common SDM variables do not match those described by physiologically relevant variables

If both the SDM variables themselves and the spatial patterns of climate they describe are different to physiologically relevant variables, we may conclude that the SDM variables are distal predictors of species distributions and caution should be applied when using these variables, particularly in studies of plant responses to climate change.

We focus only on plant species to provide a more complete and comparable analysis and because climate is widely accepted as the most dominant influence on plant distributions (cf. Box, 1981; Woodward, 1987). Further, as primary producers, plant distributions will influence resource availability at higher trophic levels, which in turn has important implications for the conservation of species further up the food chain (Hadded et al., 2009). As SDMs are used routinely to assess species distributions in the context of climate change (Austin & Van Niel, 2011), we analyse climate variables associated directly with a changing climate (Collins et al., 2013) and which are known to influence plant distributions (Austin & Van Neil, 2011), namely temperature and water availability (Körner et al., 2016).

While we acknowledge that factors such as dispersal and biotic interactions can also exert strong influence on species distributions (Gallien et al., 2015; Shea & Chesson, 2002), consideration for these is beyond the scope of this study. We hope to aid the effective parameterisation of the climatic component of SDMs, especially to meet demands to predict accurately species responses to climate change.

2 | METHODS

2.1 | Data sources

We compiled data from the peer-reviewed literature on species distributions and physiology. We performed two literature searches:

1. To source studies from the SDM literature, we used the search terms TS = (bioclimatic AND climate variables) AND TS = (species distribution OR niche) in ISI Web of Science (http://www.webofknowledge.com). This returned 343 papers (December 2017) which were sorted by relevance and individually assessed and selected for further scrutiny if the study: (a) examined the distribution of at least one plant species using climatic variables and SDM techniques; (b) was not a literature review or general discussion paper; and (c) did not as a primary aim compare how different variable types affect modelling results. Methods of the 150 qualifying studies were inspected to determine the climate variables used in each case. Studies examining the distributions of both plant and non-plant species were retained, as there were no instances in which plant species were modelled using different environmental variables to other species. We documented the full set of climate variables used in the final models and not just those found to affect species distributions. Herein, we refer to any variables sourced from the SDM literature as the "SDM" or "bioclimatic" variables.
2. To source studies from the physiological literature, we performed a systematic search in ISI Web of Science (http://www.webofknowledge.com) using the following search criteria: "experiment AND plant AND physiological AND response AND climate." This returned 245 papers (January 2019) which we sorted by relevance. We included the first 150 studies identified in this way to match the sample size of the species distribution studies. Further details of the physiology literature are provided in Appendix S2. Each study was inspected, and all climate variables found significantly or insignificantly to affect plant physiology (e.g., growth, reproduction, survival) were recorded. In cases where experimental treatments were delivered over unspecified phenological stages, but occurred when the otherwise unmanipulated environmental variables were conducive to plant growth, we defined the temporal scale of the final variable as "during the growing season." We grouped soil water content into a single variable (for each unique time period of measurement), regardless of the way this was determined in the study (e.g., gravimetrically, volumetrically) as individually the variables would be very highly correlated and would not provide meaningful additions to the physiology list if separated. There were no other cases where the grouping of variables was necessary. Herein, we refer to any variables identified from the physiology search as the "physiology" or "physiological" variables. Full details of the physiology variables can be found in the Appendix S1. A variable could be classed as both an "SDM" and a "physiology" variable if it was used to model the distribution of a plant in one of the SDM studies and also found to be physiologically relevant in a study from the plant physiology literature.

2.2 | Analysis

To identify the 10 most frequently used variables from each of the two searches, we summed the number of times each unique climate variable was used in their respective literature and sorted the results from highest to lowest. Final rankings of the physiology variables were calculated by dividing these frequencies (significant) by the number of times each variable was used (significant + insignificant) in the 150 papers reviewed. This accounts for ease of manipulation of these variables within an experimental setting, but a further limitation is that our literature search was non-exhaustive and variable rankings may therefore be sensitive to studies selected. We therefore performed a post hoc sampling with replacement procedure to test for the robustness of variable ranks. We generated 999 new samples and tested for concordance between the ranking order of the top 10 variables in each of the new samples and our original top 10 physiology variables using Kendal's *W* test (Tate & Clelland, 1957).

Studies modelling distributions of a greater number of species may use more general climate variables, so we investigated whether use of the top 10 SDM variables was influenced by species number, using a generalized linear model (GLM). As variable use was represented as either 0 (false) or 1 (true), a binomial error distribution and logit link function were used. Species number was logarithmically transformed to reduce heteroscedasticity. Eight studies were excluded from this analysis as the species number was not stated.

To produce global maps of climate variation for the top 10 SDM and physiology variables, we downloaded six-hourly data from the National Oceanic and Atmospheric Administration (NOAA) NCEP/NCAR Reanalysis (Kalnay et al., 1996) and daily data from the CPC Unified Precipitation Project gridded global climate databases (https://www.esrl.noaa.gov/psd/). These data were resampled and processed to construct and map (averaged over the period 2000–2017) each of the top 10 SDM and physiology variables at 2.5° resolution (see Appendix S2 for further details on data download and processing and Appendix S3: Figures S3 and S4, for global maps of each variable).

We sought next to provide statistical comparison between the climatic conditions described by the SDM and physiology variables. However, climate variables are often correlated with one another, and in consequence, even if the variables are different, the spatial patterns of those most frequently used in SDMs may capture in aggregate the spatial patterns of the physiological variables. We followed a two-step process in order to compare the SDM and

physiology variables: (a) principal component analysis (PCA) on both variable sets; and (b) multiple regression analysis of SDM principal component scores using scores from physiology principal components (PCs) 1–3 as predictors.

Principal component analysis can be used to reduce dimensionality in a dataset and indicate which variables contain the most information (King & Jackson, 1999). Here it allows us to determine which aspects of climate variation are described by the SDM and physiology variables. We performed two PCAs to identify which climate variables contributed most to the overall variation in conditions described by the top 10 SDM and physiology variables. Total annual precipitation and mean annual temperature were not included in the analyses as they featured in both top 10 lists and so it was not necessary to examine the spatial differences between the SDM and physiology studies for these variables. Data were scaled to account for differences in units among each variable set, and a scree plot was used to determine how many PCs to retain from each PCA (Appendix S3: Figure S2). For both the SDM and physiology variables, we retained the first three PCs. We analysed the variable loadings for PCs 1–3 for both variable sets to determine the aspects of climate they described.

It is not possible to compare PCs in a like-for-like way between variable sets. PC1 for the SDM variables, for example, may correlate poorly with PC1, but well with PC2 of the physiology variables so that collectively the PCs from the two sets of variables may describe similar trends in global climate variation. To assess similarity between the climate variation described by the physiology and SDM variables, we therefore performed three multiple regression analyses on scores of each of the SDM PCs using the scores for the physiology PCs 1–3 as predictors (Appendix S3: Figure S5). To determine the variance unexplained collectively by the multiple regressions, we calculated the squared residuals for each regression and mapped the square root of the minimum of these residuals, thereby revealing where discrepancies in the spatial patterns of climate captured by the two sets of variables were greatest (Figure 3).

All data analyses were conducted using the statistical programme R (R Core Team, 2018).

3 | RESULTS

3.1 | Climate variables

Two hundred and eighty-nine unique climate variables were identified from the 150 SDM studies (Appendix S1). The 10 most commonly used were (a) annual mean temperature (98 studies); (b) total annual precipitation (87); (c) precipitation seasonality (70); (d) temperature seasonality (69); (e) precipitation of the driest period (68); (f) minimum temperature of the coldest period (66); (g) mean diurnal range (65); (h) isothermality (63); (i) precipitation of the coldest quarter (60) and (j) temperature annual range (60) (Table 1). All the top 10 SDM variables were from the standard list of 19 "Bioclim" variables available from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Forty-four studies (29%) used the full set of 19 WorldClim variables in their models (Appendix S3: Figure S1). Ninety-six unique climate variables were identified from the 150 plant physiology studies (Appendix S1). After accounting for non-significance, the 10 most commonly used variables were (a) soil water content during the growing season (38); (b) mean growing season temperature (29); (c) growing season precipitation (17); (d) total summer precipitation (11); (e) total annual precipitation (7); (f) growing season length (6); (g) maximum temperature during the growing season; (h) mean annual temperature (5.4); (i) mean summer temperature (5); and (j) summer soil water content (5) (Table 2).

We found strong concordance between variable ranking in the original and new samples (mean statistics for n = 999: W = 0.76, p = <0.01; p-value range: 1.22×10^{-14}, 1.62×10^{-1}; W statistic range: 0.69, 0.83). This supports the robustness of the ranking order of our physiology variables.

Total annual precipitation and mean annual temperature were the only variables that featured in both the SDM and physiology top 10 lists. Of the top 10 SDM variables, six captured variation or extremes of temperature and four captured variation or extremes of precipitation. The top 10 physiology variables were more diverse in the aspects of climate that they describe and placed greater emphasis on water availability. Soil moisture content was the most commonly identified physiology variable yet was only included in one SDM study. The timing of climatic events within the growing season was important to five of the physiology variables but was not explicitly featured in any of the SDM variables.

3.2 | Spatial patterns

Comparison of global maps depicting the mean values for the SDM and physiology variables indicate that the spatial patterns of climate they describe are dissimilar. For example, global variation in growing season soil moisture content, the top physiology variable, was not matched by any of the SDM precipitation variables; growing season soil moisture content showed a more patchy distribution, particularly in the Northern Hemisphere, whereas variation in the SDM precipitation variables generally radiated out from the equator. Similarly, temperature seasonality and maximum temperature during the growing season, the variables ranking fourth and seventh in the SDM and physiology top 10, respectively, showed clear differences in spatial variation despite both describing temperature indices of climate. Maximum temperature during the growing season captures climatic variation more independently of equatorial influence than temperature seasonality and acknowledges that extreme high temperatures (>35 C) will be detrimental to plant growth. The physiology variables appeared to show greater spatial heterogeneity in climatic variation, particularly for the temperature-related variables. The physiology variables highlighted areas with climates distinct from that of the general trend in the surrounding area, such as along the west coast of South America, whereas the SDM variable appeared to smooth out these nuances. Global maps of the top 10 SDM and physiology variables (averaged for the period 2000–2017) are shown in Appendix S3: Figures S3 and S4.

TABLE 1 Summary of the top 10 climate variables used in plant species distribution modelling studies, including variable descriptions and temporal scale of data required to calculate them. "BIO" indicates the variable's WorldClim reference code: http://www.worldclim.org/bioclim. Significance levels refer to results of a general linear model of whether use of each variable was influenced by the number of study species in the model

Rank	Variable name	Variable description	Temporal scale of data to calculate climate variable	Number of studies	Relationship to species number
1	Annual mean temperature (BIO1)	The mean of all weekly mean temperatures over a year	Monthly	98	0.66
2	Total annual precipitation (BIO12)	The sum of all weekly precipitation values over a year	Monthly	87	0.02*
3	Precipitation seasonality (coefficient of variation) (BIO15)	The variation in weekly precipitation totals over a year based on the standard deviation of weekly total precipitation	Monthly	70	0.25
4	Temperature seasonality (coefficient of variation) (BIO4)	The temperature variation over a year based on the standard deviation of weekly average temperature	Monthly	69	0.26
5	Precipitation of driest period (BIO14)	Total precipitation falling in the driest week or month of the year	Monthly	68	0.06
6	Minimum temperature of the coldest period (BIO6)	The minimum temperature in the coldest week or month of the year	Monthly	66	0.52
7	Mean diurnal range (BIO2)	The mean of the weekly temperature ranges over a year	Monthly	65	0.02*
8	Isothermality (BIO3)	Quantifies the day-to-night temperature oscillations relative to the summer-to-winter (annual) oscillations (BIO2/BIO7)	Monthly	63	0.03*
9=	Precipitation of coldest quarter (BIO19)	Total precipitation falling in the coldest quarter (13-week period) of the year	Monthly	60	0.14
9=	Temperature annual range (BIO7)	The temperature variation over a year, calculated as the difference between the maximum temperature of the warmest period and the minimum temperature of the coldest period (BIO5-BIO6)	Monthly	60	0.04*

*$p \leq 0.05$.

TABLE 2 Summary of the top 10 climate variables used in the plant physiology studies, including variable descriptions and the temporal scales of data required to calculate each variable

Rank	Variable name	Variable description	Temporal scale of data to calculate variable	Number of studies
1	Soil water content during growing season	The amount of water in the soil during the growing season (including volumetric, fractional and gravimetric calculations)[a]	Daily[b]	38
2	Mean growing season temperature	The average daily temperature during the growing season[a]	Daily	29
3	Total precipitation during growing season	Total precipitation falling during the growing season[a]	Daily[b]	17
4	Total summer precipitation	Total precipitation falling during the summer[c]	Daily	10.1 (11 significant)
5	Total annual precipitation	The sum of all precipitation values over a year	Daily	7
6	Length of growing season	The entire period (in days) in which plant growth can theoretically take place (Carter, 1998) over the course of 1-year[a]	Daily[b]	7
7	Maximum temperature during the growing season	The maximum temperature during the growing season[a]	Daily	6
8	Mean annual temperature	See BIO1. The mean of all weekly mean temperatures over a year	Weekly	5.4 (7 (significant)
9	Mean summer temperature	The mean temperature during the 3-month (91-day) Summer period	Daily	5
10	Summer soil water content	The average amount of water in the soil during the 3-month Summer period[c]	Daily	5

[a]For the purposes of calculation, we define growing season as any period where daytime temperatures are >5 C and <35 C and precipitation is >half evapotranspiration for five consecutive days.
[b]The definition of growing season used in this study requires daily climate data, but temporal scale may vary for other definitions. For example, if growing season is defined as a period of months, monthly average data may be sufficient; if growing season is defined by date of snow release, daily climate data will be required.
[c]Definitions in original study may vary, but explicitly state "summer." For the purposes of calculation, we define summer as 1st June–31st August (Northern Hemisphere) or 1st December to 2nd March (Southern Hemisphere).

3.3 | Principal component analyses

The first three components for the SDM and physiology variables explained 86% and 94% of the variance, respectively (Tables 3 and 4). For the SDM variables, PC1 explained 58% of the variation and was most strongly correlated with temperature seasonality (−0.43) and temperature annual range (−0.43). Mean diurnal range (−0.41) and isothermality (0.40) also loaded relatively strongly in opposing directions. In general, coastal areas scored higher than their adjacent continental space, suggesting that this PC describes well the continentality of an area (Figure 1). PC2 explained an additional 23% of the cumulative variation in SDM variables and was correlated most strongly with precipitation seasonality (0.66), precipitation of the driest period (−0.55) and precipitation of the coldest quarter (−0.37). PC3 was correlated most strongly with precipitation of the coldest quarter (−0.62), precipitation seasonality (−0.51) and precipitation of the coldest quarter (0.48) (Table 3).

For the physiology variables, PC1 explained 67% of the variation and was most strongly correlated with growing season length (0.40), growing season soil moisture (0.39) and mean growing season temperature (0.39). PC2 explained an additional 24% of the cumulative variation and was positively correlated with summer soil water content (0.68) and negatively correlated with mean summer temperature (−0.43). PC3 was most strongly correlated with growing season precipitation (−0.54) and summer soil water content (0.51) (Table 4). Overall, PC scores appear to describe the tropicality of an area. Each PC for the physiology variables captures a balance between temperature and soil moisture variables, rather than considering temperature and water variables more independently as seen for the SDM variables.

Figures 1 and 2 show the global variation in climate conditions as described by the first three PCs for SDM and physiology variables.

Although PCA can identify which aspects of climate describe most variation in the raw data, PC scores are not directly comparable across different variable sets. The minimum residual scores ranged from 0.000024 to 1.80 (Figure 3). Areas with the largest residual differences included parts of Central Africa, north-eastern South America and Southeast Asia, including the islands of Indonesia. Many of these areas experience tropical climate (cf. Geiger, 1961; Kottek, Grieser, Beck, Rudolf, & Rubel, 2006), reflecting the differences in the aspects of climate described by the SDM and physiology PCs; each SDM PC described independently either aspects of climate related to precipitation or to temperature, whereas all PCs for the physiology variables described aspects

of climate associated with tropicality and the mutual availability of water and temperature. This analysis confirmed that in some areas, the SDM and physiology variables capture different aspects of climate variation and this could have important implications for the reliability of SDM predictions.

3.4 | Correlation with species number

Individually, total annual precipitation, mean diurnal range, temperature isothermality and temperature annual range (rankings 2, 7, 8 and 9, respectively) were more likely to be used with an increasing number of study species (GLM, $p = 0.02$, $p = 0.02$, $p = 0.03$, $p = 0.04$) (Table 1). When considered together, however, use of at least one of the SDM top 10 variables was not found to be related to study species number (GLM, $p = 0.79$). The likelihood of one of the top 10 physiology variables being reported as significant in the physiology literature was not related to the number of study species (GLM, $p = 0.68$).

4 | DISCUSSION

4.1 | Variable selection as a predictor of plant distributions

The climate variables used in SDMs are assumed to reflect the physiological constraints on the study species that affect where they can survive in the wild (Kearney & Porter, 2009). Proximal variables represent a direct link between climate and physiology (Austin, 2002; Jackson et al., 2009) and as physiological limits are inherent traits, their influences on a species' distribution are more likely to be conserved in time and space (Austin, 2002, 2007). Distal variables, however, correlate indirectly to species' physiology through their relationship to the proximal variables they replace (Merow et al., 2014). Although distal variables may provide a good "mean field approximation" for proximal predictors under existing climates (Bennie et al., 2014), it cannot be assumed that this relationship will be conserved in time and space, and in consequence, the use of distal variables in predictive models is questionable. Physiological variables may therefore be more robust predictors of species distributions in novel climates and locations (Austin, 2002).

The results from our literature review affirm our first hypothesis: the climate variables used in SDMs are different from those known directly to influence plant physiology. Most notably, the top physiology variables highlight an important role of soil moisture content and suggest that the growing season is a critical time period for climatic influence on plants. The top 10 SDM variables, however, are skewed towards the use of temperature indices of climate, neglect the influence of soil water availability and mostly capture annual or seasonal trends rather than the timing of climate events within important periods of plant growth and development. In this way, the most common SDM variables are considered to be distal indicators of plant distributions and may struggle to replicate physiologically relevant aspects of climate variation (Elith & Leathwick, 2009).

Lack of consideration of soil moisture content is an important omission from the top SDM variables. Almost every physiological process in plants is affected directly or indirectly by water supply (Kramer & Boyer, 1995), and soil water conditions have been shown to be a primary determinant of small-scale plant distributions (Engelbrecht et al., 2007; Tromp-van Meerveld & McDonnell, 2006) and overall habitat type (Moeslund et al., 2013). Schietti et al. (2014), for example, found that 82% of the variation in plant composition in Amazon terra firme forest could be explained by the depth of

TABLE 3 Summary of principal component analysis for SDM variables, including variable loadings for principal components 1–3

Variable name	PC1	PC2	PC3
Precipitation of the driest period	0.227	0.553	0.054
Precipitation seasonality	0.013	−0.660	−0.514
Precipitation of the coldest quarter	0.316	0.374	−0.617
Mean diurnal range	−0.411	−0.041	−0.036
Isothermality	0.396	−0.019	−0.284
Temperature seasonality	−0.433	0.197	−0.185
Minimum temperature of the coldest period	0.384	−0.206	0.484
Temperature annual range	−0.434	0.187	−0.050
Standard deviation	2.158	1.343	0.661
Proportion of variance	0.582	0.226	0.055
Cumulative proportion of variance	0.582	0.808	0.862

TABLE 4 Summary of principal component analysis for physiology variables, including variable loadings for principal components 1–3

Variable name	PC1	PC2	PC3
Growing season soil moisture content	0.393	0.264	−0.235
Growing season length	0.404	0.105	0.049
Mean growing season temperature	0.390	−0.235	0.351
Summer soil water content	−0.062	0.676	0.512
Maximum growing season temperature	0.385	−0.236	0.495
Growing season precipitation	0.369	0.298	−0.540
Total summer precipitation	0.372	0.283	0.050
Mean summer temperature	0.321	−0.427	−0.133
Standard deviation	2.317	1.397	0.487
Proportion of variance	0.671	0.244	0.030
Cumulative proportion of variance	0.671	0.915	0.944

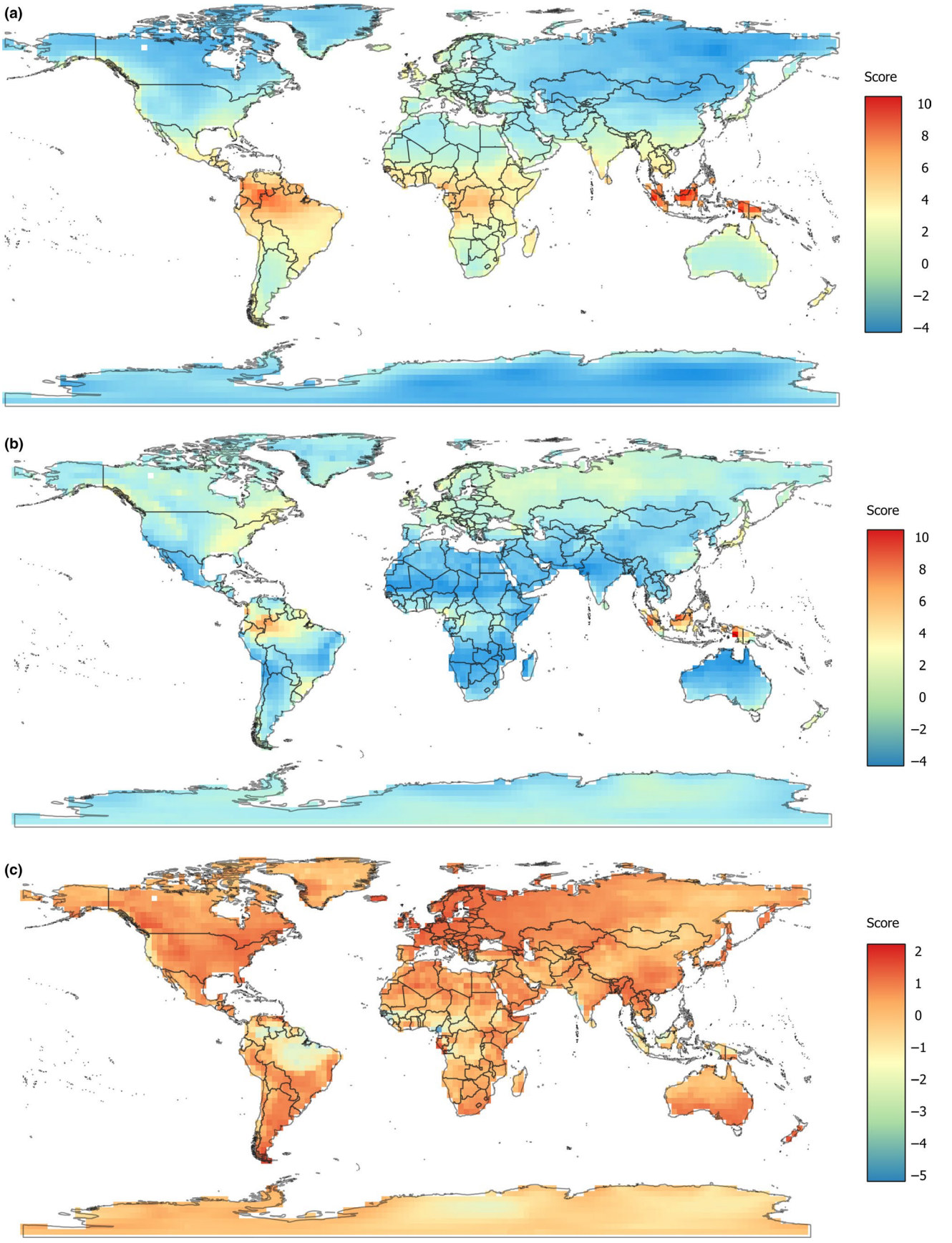

FIGURE 1 Global maps of climate variation as described by the first three principal components (PCs) associated with the SDM variables: (a) PC1; (b) PC2; (c) PC3

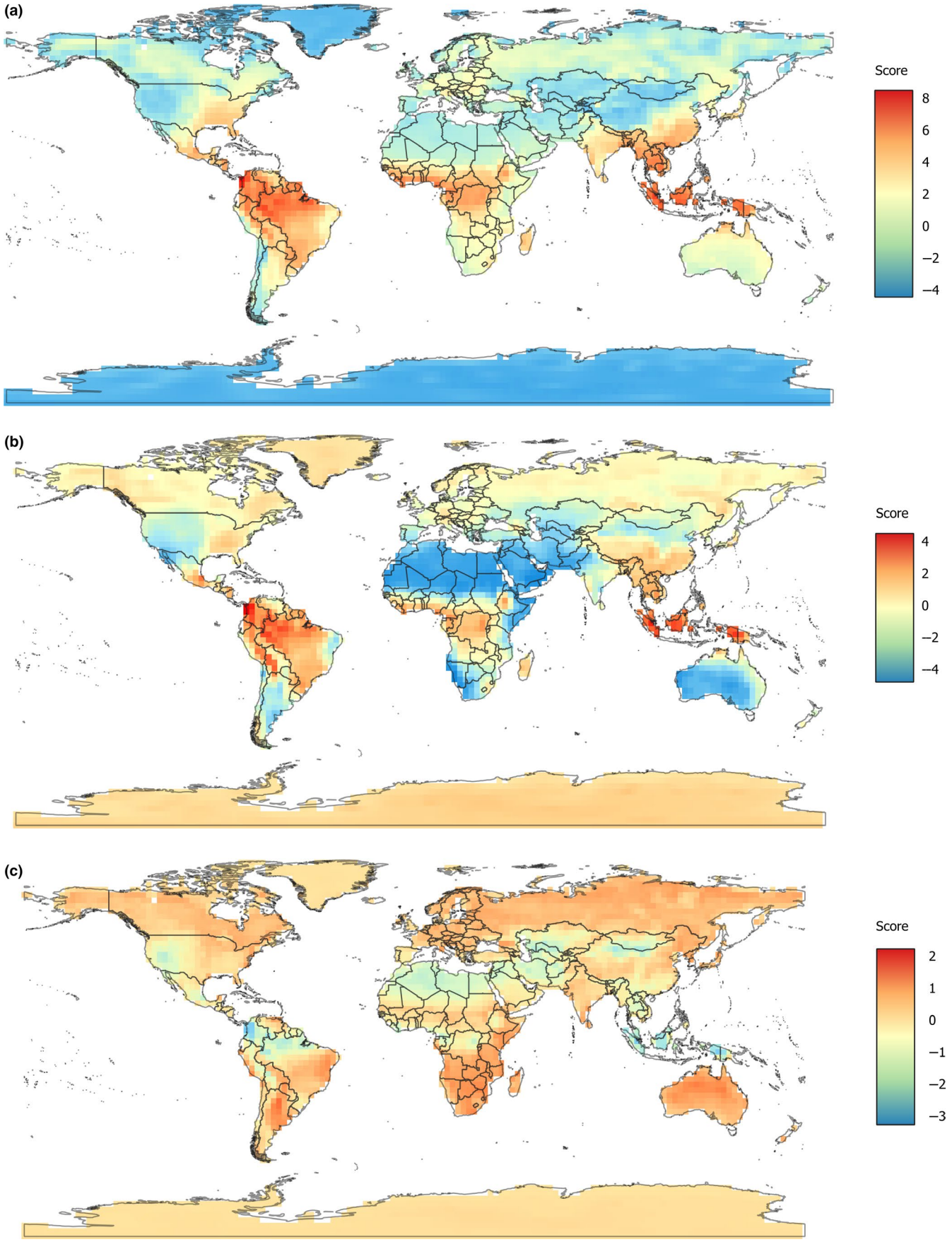

FIGURE 2 Global maps of climate variation as described by the first three principal components (PCs) associated with the physiology variables: (a) PC1; (b) PC2; (c) PC3

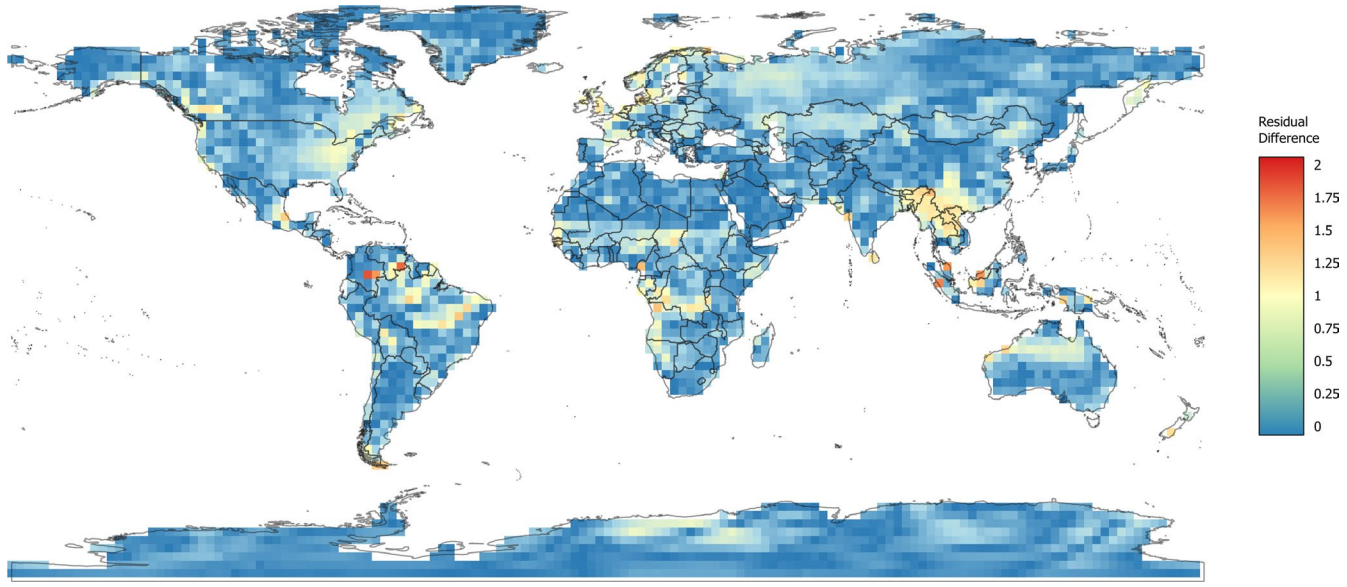

FIGURE 3 Global map of the minimum residual differences from multiple regression analyses of SDM principal components 1–3 using scores from principal components 1–3 for the physiology variables as predictors

the water-table, and diversity in plant communities from the South African Fynbos (Araya, Gowing, & Dise, 2010) to English meadows (Silvertown, Dodd, Gowing, & Mountford., 1999) has been attributed to hydrological niche separation.

Precipitation is often selected as a distal predictor for soil moisture (e.g., Austin & Van Niel, 2011) and, indeed, four of the top 10 SDM variables related to precipitation. However, precipitation has been shown to be a poor proxy for soil moisture conditions (Piedallu, Gégout, Perez, & Lebourgeois, 2013) and may therefore fail accurately to capture the amount of water that ultimately becomes available to plants (Dilts, Wesiberg, Dencker, & Chambers, 2015). The discrepancy between precipitation and soil moisture variables may become increasingly important at finer spatial scales, where topography has greater influence on soil water content (Daws, Mullins, Burslem, Paton, & Dalling, 2002; Maclean, Bennie, Scott, & Wilson, 2012) or in transition zones between wet and dry climates where evaporation is high and feedbacks between soil moisture and precipitation occur (Koster et al., 2004). Substituting soil moisture variables with precipitation surrogates could therefore threaten the reliability of SDMs (Weltzin et al., 2003), and indeed, explicitly incorporating soil moisture predictors into SDMs for plants has been suggested as a way to increase the reliability of subsequent range predictions (e.g., Whitehead, 2001).

Another feature of the physiology variables is that the growing season emerges as a critical period for climate influence on plants; five of the top 10 physiology variables featured the growing season, but this was not explicit in any of the top 10 SDM variables. This omission carries similar issues to those discussed for soil moisture, as without consideration for this important period for plant growth the SDM variables may fail to capture the aspects of climate that limit plant distributions. For example, although mean annual temperature may be correlated with mean growing season temperature, the former may obscure periods of high or low temperatures when plants are most sensitive to environmental conditions or have greater requirements for warmth. As with the use of precipitation as a proxy for soil moisture content, the use of distal predictors that consider monthly or yearly climate averages rather than conditions specifically within the growing season period may have negative implications for the reliability of range predictions.

The PCAs highlight that variation among the top 10 physiology variables can be described by aspects of climate related to tropicality, particularly the combined strength of accumulated temperature, soil moisture content and precipitation during the growing season. Variance among the SDM variables, however, is described by factors reflecting the variability and extremes of temperature and precipitation throughout the year and could be considered to define climate continentality.

The PCA results suggest that, physiologically, it is important that climate variables consider the mutual availability of temperature and water (i.e., "better together") whereas the SDM variables describe the ranges or extremes in these aspects of climate (and usually model them independently of each other). Most plant phyla are known to have evolved during a "tropical planet" (Benton, 1993) and high niche conservatism in plants (Prinzing, 2001; Romdal, Araújo, & Rahbek, 2013) means that many species are likely to have retained a tropical affinity (Wiens & Donoghue, 2004). Our results concur with this hypothesis as climate variables indicating tropicality, particularly combinations of temperature and water, were found to be physiologically important to plants.

Our second hypothesis was also supported. By calculating and mapping globally the minimum residual differences between PC scores for the SDM and physiology variables, we show that the spatial patterns of climate variation described by the most commonly used SDM variables do not match those described by physiologically

relevant variables. We conclude that the top 10 SDM variables are distal indicators of species distributions.

Residual differences were greatest in areas where precipitation regimes or the mutual availability of temperature and water become more important to the classification of climate, which confirms that the SDM variables are poor proxies for physiological variables that relate to water availability, particularly soil moisture content and the timing of rainfall within the growing season. Areas of hot desert and polar climates (as defined by the Köppen-Geiger climate classification system—Geiger, 1961; see Kottek et al., 2006 for updated global map), however, were, in general, similarly described by both sets of variables. These are areas of temperature extremes (although in opposing directions) which suggests that once a certain temperature threshold is reached, average climate data can adequately capture physiologically limiting conditions and may be good substitutes for more proximal variables in these cases.

Importantly, many areas with larger residual differences are considered conservation priorities (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000) due to a combination of high biodiversity (Mittermeier, Myers, Thomsen, Da Fonseca, & Olivieri, 1998) and vulnerability to climate change (Malcolm, Liu, Neilson, Hansen, & Hannah, 2006). For example, there were large differences in scores in the Indo-Burma biodiversity hotspot in tropical Asia, as well as the tropical rainforest regions of South America and Indonesia, which all experience consistently high rainfall and warm temperatures throughout the year. There were also large residual differences in the Himalayan, Appalachian and Scandinavian mountain regions, which may reflect the fact that soil moisture content can be highly spatially (le Roux, Aalto, & Luoto, 2013) and temporally (Kemppinen, Niittynen, Riihmäki, & Luoto, 2018) heterogeneous and may show weak correlations to precipitation in mountainous terrains (le Roux et al., 2013). It may therefore be especially important to consider using more proximal climate variables when studying species distributions in tropical or mountainous areas, particularly if the results will inform conservation policy or planning decisions to protect global biodiversity.

4.2 | Variable selection in a changing climate

Species distribution models have become a popular tool among ecologists and conservation biologists to predict how species might respond to climate change (Pearson & Dawson, 2003). Indeed, in the studies we examined, nearly one-third (48/150) aimed to predict species response to climate change as their primary objective and most referred to the application of SDMs for this purpose. As the climate warms further and the results of previous change become more evident, the role of SDMs to predict the impacts of climate change on species distributions and aid conservation strategies is likely to grow and many authors have highlighted the need to account for climate change in protected area design (Araújo, Cabez, Thuiller, Hannah, & Williams, 2004; Hannah et al., 2007) and to assess the best locations to protect species of conservation priority (e.g., 20082008; Porfirio et al., 2014).

When applying SDMs to climate change studies, the variables selected for modelling are assumed to be good predictors of a species' range in a new time and place. Until a forecasted future climate is realized, however, it will be impossible to determine the accuracy of these predictions. A major advantage of using proximal climate variables is that their direct link to physiology and therefore species distributions can be quantified and is unlikely to change significantly over the modelled time period (acknowledging that although local adaptation may occur), it is unlikely to match the rate of climate change (Davis & Shaw, 2001). This means proximal variables are likely to be more reliable indicators of future species distributions.

The distal variables used often in correlative studies may provide less robust estimates of future ranges as their correlations to proximal variables cannot confidently be extrapolated over space or time (Elith & Leathwick, 2009). Unquantified additional factors may support a relationship between a distal variable and species distributions in the present day. The contribution of these "hidden" variables may break down or cease to apply in new locations or over new time periods and thus lead to unreliable predictions from SDMs. Basing future range predictions purely on changes to a distal climate variable may therefore be problematic if the climatic component of the original correlation does not match physiologically relevant patterns of variation.

We show here that, on a coarse-scale, the spatial patterns of climate variation described by the SDM variables differ from the key physiology variables. Although we cannot prove that our physiology variables would be appropriate indicators of changes in species distributions at the level at which the organism responds, they maintain a justifiable link to limiting processes over both spatial and temporal scales that cannot be assumed for the SDM variables. Selection of more proximal variables could help to ensure that the predictions from SDMs which inform important conservation decisions are as accurate and reliable as possible and do not over- or under-estimate ranges to the point where protected areas may fail to protect the species of interest.

Alongside raising the need for accurate predictions of species ranges, climate change will increase the challenges associated with modelling their distributions. For example, climate change is expected to increase the frequency and intensity of extreme weather events (Collins et al., 2013) which can advance the change in species composition in response to altered environmental conditions (Jentsch, Kreyling, & Beierkuhnlein, 2007). The possibility of more extreme weather supports the use of physiologically relevant climate variables as correlations between proximal variables that reflect climatic events and those describing averaged trends may weaken or break down in more unpredictable climates. Fay, Carlisle, Knapp, Blair, and Collins (2003), for example, show that increased variability of rainfall, without reduction in the overall rainfall amount, can reduce above ground net primary productivity in a tall-grass prairie in Kansas.

Similarly, Orlowsky and Seneviratne (2012) report that predicted future seasonal extremes of temperature scale with changes in global annual mean temperature by a factor of more than two,

with the consequence that limiting thresholds of temperature may not be captured in averaged data (e.g., Parker & Abatzoglou, 2017). Although recent range expansions have been attributed to rises in mean annual temperatures (Wilson et al., 2005), this means that species responses to distal predictors are likely to be lagged, and the absolute number of days outside of their physiological tolerance may increase on a much shorter time-scale (Parmesan, Root, & Willig, 2000). Late frosts or summer heatwaves, for example, are likely to impact species almost immediately if these affect their ability to survive, grow and reproduce and proximal variables would be able to capture these tolerances and track changes to species distributions occurring in "real-time." This may also provide information on changes to species distributions on a time-scale that is more relevant to conservation decision-making and facilitate the development of proactive management strategies.

A lengthening of the growing season is another expected result of climate change (Jentsch et al., 2007) and has already been observed in higher latitudes (Menzel & Fabian, 1999). We have identified that climate conditions during the growing season have important physiological implications for plants and it could therefore become even more crucial for variables explicitly to consider climate conditions within this period in the future. Mosedale, Wilson, and Maclean (2015), for example, show that although climate change may generally improve growing conditions for grapevine, the risk of frost damage during spring increases under many scenarios due to advancement in the timing of budbreak. A longer growing season could therefore leave agricultural crops more vulnerable to extreme events which currently tend to occur outside of this critical period (Lesk, Rowhani, & Ramankutty, 2016). To base crop selection decisions on SDMs that do not consider how climate change may alter conditions during the sensitive growth stages of plants is a risk to livelihoods and food security.

Understanding the proximal drivers of the natural or farmed distributions of agricultural crops could be important to maintain yields in species which are threatened by a changing climate (e.g., Ray, Gerber, MacDonald, & West, 2015). Crop SDMs that use proximal climate variables may be more appropriate to inform smart future land use planning and crop decision-making based on species' environmental optima and tolerances. Similarly, proximal variables may be better able to suggest how management practices could be adjusted to grow new crops, such as through the use of greenhouses to raise growing season temperatures, or to mitigate the impacts of a changing climate on yields, such as through the use of irrigation in areas which become more arid.

4.3 | Using physiological variables

Species distributions are shaped ultimately by interrelations between climate conditions and biological traits (Sterck, Markesteijn, Toledo, Schieving, & Poorter, 2014). In their study of North American tree species, Morin, Augspurger, and Chuine (2007), for example, show how physiological responses to climate conditions constrain species' ranges, particularly through impacts on phenological processes such as fruit ripening and flowering. Similarly, Thuiller, Lavorel, Midgley, Lavergne, and Rebelo (2004) showed that gradients in climate explain almost all variation in the niche distribution of 88 flowering plants of the Cape Floristic Region, South Africa, with niche differentiation characterized by differences in traits such as leaf area and timing of initiation of flowering. The variables used in SDMs attempt to capture, at the population-level, the effect of many individuals responding to climatic pressures and must therefore offer a good "mean field approximation" for biological processes that determine whether a species can survive, grow and reproduce in an area (Bennie et al., 2014). Proximal variables are intimately tied to biological process of the study species and as such, may provide better approximations of the climatic requirements of a species that influence their distributions (Kearney & Porter, 2009).

The physiology variables identified in this study derive from experimental studies, where plant responses to climate are often quantified very close to the individual (within metres or even less). We recognize that in modelling these variables at coarse-resolution, conditions may differ significantly from those experienced by plants (Bramer et al., 2018; Tabor & Williams, 2010) but importantly, and unlike the SDM proxies, these variables retain a direct link to physiological processes. Our inability to construct the physiology variables at a fine-resolution highlights the current limitations to effectively mapping species distributions with available climate data. Physiological variables may be excluded from SDMs because the data required to construct them are unavailable (Kearney & Porter, 2009) and it is likely that our list of the top 10 SDM variables reflects these data deficiencies; global climate surfaces for Bioclim variables are readily downloadable at 1 km resolution whereas no equivalent dataset exists for the physiological variables (Bramer et al., 2018).

Models which allow microclimate conditions to be estimated from coarse-grid data do exist. The microclimate model of NicheMapper, for example, can be used to predict hourly local microclimates from macroscale data (Kearney, Shamakhy, et al., 2014). However, a number of climate forcing variables are required as inputs and the reliability of microclimate estimates may be compromised if hourly data are unavailable and therefore obtained by interpolation. Readily available datasets of ecophysiologically meaningful variables, or fine spatial and temporal climate data, which allow such variables to be derived (Kearney, Isaac, & Porter, 2014), are therefore much needed. To achieve this, it will be crucial to expand monitoring networks for physiologically relevant climate variables or further develop and implement methods that downscale coarse climate data to predict local variability in these conditions (e.g., microclima (Maclean, Mosedale, & Bennie, 2018); NicheMapper (Kearney, Shamakhy, et al., 2014); NicheMapR (Kearney & Porter, 2017); Maclean, Suggitt, Wilson, Duffy, & Bennie, 2017).

To predict how climate change may impact species distributions, physiological datasets for potential future climate scenarios will also be required. This may be possible through the use of statistical weather generators which produce multiple statistically plausible simulations of weather at temporal resolutions (e.g., Ivanov, Bras, & Curtis, 2007) which could in aggregate be used to

generate probabilistic estimates of physiologically relevant variables. Importantly, this approach to modelling future climate conditions can capture changes to climate extremes and variability (Semenov & Barrow, 1997) and has been applied with success in the agricultural literature in studies of crop suitability (e.g., White, Hoogenboom, Kimball, & Wall, 2011; Holzkämper, Calanca, Honti, & Fuhrer, 2015) and future climatic risk (Mosedale et al., 2015). Meanwhile, a useful next step would be to test the ability of our top 10 physiological variables to predict the current distributions of some species.

5 | CONCLUSION

Species distribution models should be constructed using aspects of climate to which the study species is known or most likely to respond (Bramer et al., 2018; Suggitt et al., 2017). We have shown here that the most commonly used SDM variables often neglect important physiological factors and, in particular, that soil moisture content and the timing of climatic events during the growing season should feature more explicitly in the climate variables used in plant SDMs. We echo other researchers in that climate variables should be justified based on the physiology of the study species (e.g., Austin & Van Niel, 2011), but more specifically, that they should be closely related to these proximal mechanisms. This is likely to be particularly important when predicting species distributions in tropical or mountainous environments, where we suggest that the results of SDMs that use distal variables are interpreted with more caution.

Data deficiencies are often considered a limiting factor for the use of proximal variables in SDMs. With the advent and recent improvements in remote sensing technology, there are more opportunities than ever before to measure physiologically relevant variables and use these data to model species distributions (e.g., Kemppinen et al., 2018). Wherever possible, new technologies should be exploited to expand physiologically relevant climate datasets as this could help prevent variable use being compromised based on data availability. We also urge climatologists to consider, as a matter of priority, the development of high-resolution climate surfaces for physiologically meaningful variables. The ability of statistical weather generators to provide information on physiological conditions for possible future climate scenarios should also be explored. There is a growing demand for robust predictions of species distributions and taking steps to make physiologically relevant climate data more widely available for use in SDMs could support the best conservation decisions to protect global biodiversity as the climate changes.

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DATA ACCESSIBILITY

Please refer to Appendix S1 and Appendix S2 of the Supporting Information. The R script used to build our analysis has been released as an R package (climvars) on GitHub (https://github.com/ilyamaclean/climvars).

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BIOSKETCH

The authors are interested in conducting and applying ecological research to find practical solutions to environmental problems. They hope to advance species distribution modelling techniques to bear on important issues in ecology and conservation biology such as land use strategies. Current research includes the study of climate change impacts on plant distributions and the associated risks and benefits this may bring to the agricultural industry.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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